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THE EVOLUTION OF THE DACETINE ANTS

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ABSTRACT

A preliminary synthesis of evolutionary studies of certain morphological and ethological characters in the ant tribe Dacetini is given. A primary trend inferred from the study of living species is the shift from epigaeic-subarboreal to cryptic terrestrial foraging. Possibly associated in the early stages of dacetine evolution with this shift was a trend toward oligophagous predation, resulting in extreme cases among modern forms in specialized feeding on collembolans. Secondary changes have occurred in hunting behavior and in a diversity of morphological features; these are described briefly. Reversed or, more accurately, "countercurrent" evolution has occurred in various phyletic lines in most of the characters of this morphological-ethological coadaptive system. Such changes are relatively short-range and usually involve only a few characters at a time. In at least some instances they have produced a local reversal in the overall dacetine trend to specialization, as with secondarily increased polyphagy in some species of Strumigenys. *Convergence to the higher dacetine morphological type has occurred independently in several other ant tribes; in at least one case* (Rhopalothrix) *ethological convergence is also evident.*

INTRODUCTION

In recent years, we have witnessed a spectacular rise in interest in comparative studies of animal behavior. Many of these studies have attempted to relate behavior of given species or higher taxa to their particular environments, to the morphology and physiology of the animals, to their systematics, and to their evolutionary history. Certainly, the integration of all these approaches should be a principal goal of the modern investigation of any group.

One important group of animals that is especially favorable for such an integrated study is that of the ants. These insects form a distinct family, the Formicidae, in the Order Hymenoptera, or wasp-like insects. The ants are still incompletely known and are rather unsatisfactorily classified, but we believe that, with more than 10,000 species and several hundred genera already described, they are roughly comparable in diversity to a taxon such as the class Aves.

As is implied by their placement among the Hymenoptera, the ants arose (apparently during the Cretaceous) from some group of wasps, probably solitary wasps allied to the living Tiphiidae. The existing ant species are all social; that is, parent adults and their offspring of all developmental stages live together in groups, called colonies. In most species the colonies inhabit more or less definitely structured nests in the soil, in plant cavities, etc. During most of the year they are composed entirely of females, which are normally divided into two basic castes, the queens and the workers, which tend to be specialized for different functions. Males appear in the colonies at certain seasons, and are important only in sexual reproduction.

The fact that nearly all human cultures have a common word meaning "ant" is a tribute to the abundance and ubiquity of these insects over the temperate and tropical parts of the earth. Their great numbers and relatively high activity rates place them among the really important transformers of energy in terrestrial environments. It is again their exceptional abundance, as well as the ease with which they may be found and cultured in the laboratory, that renders ants ideal subjects for biological study.

The most primitive ants, like their wasp ancestors, feed their larvae on many kinds of insects that they capture on plants or on the ground surface, while the adult workers themselves gain a large part of their nourishment from nectar or other sugary substances for which they forage on plants. In higher groups of ants feeding is often more specialized. Some kinds

forage almost entirely on the trunks or foliage of trees, where they may tend plant lice for their honeydew, hunt insects or both. Many types have become harvesters of seeds, and one group, the Attini, raises and eats fungi, thus engaging in the only well-established case of true crop agriculture except for that managed by mankind.

Other lines among the ants have developed predatory mass-foraging "army ant" habits that have allowed them a wider choice of prey, while still others have evolved very narrow prey preferences, such as the *Leptogenys* which feed on sowbugs (Oniscoidea), or the eyeless *Centromyrmex*, believed to capture termites in their subterranean passages. There is even one large group, the Cerapachyini, that lives by raiding the nests of other ants and feeding on their brood. To this category of specialist predators belong also the Dacetini, a tribe of nearly 200 known species belonging to the subfamily Myrmicinae, one of the nine major divisions of the Formicidae. We have not yet uncovered the relationships of the Dacetini to the other tribes of Myrmicinae; they form a phyletically isolated group, occurring mainly in the tropics and milder temperate regions of the earth. But enough is now known about them to make the Dacetini an especially instructive case history of group evolution.

In 1936 L. G. Wesson showed that the dacetine ant *Smithistruma pergandei* (Emery) has some remarkable peculiarities in its food-getting behavior. Workers of this species prey chiefly or exclusively on springtails (collembolans), which they capture by an elaborate maneuver including careful stalking followed by a sudden, trap-like closure of the mandibles. Wesson and Wesson (1939) showed that similar behavior is exhibited by a few other species of *Smithistruma* in North America. These early observations, which have been fully confirmed by later work, revealed *Smithistruma* as one of the most highly specialized of all ant genera of which the habits are known. *Smithistruma*, however, represents the end-product of but one phyletic line of the Dacetini. This large cosmopolitan tribe contains a rich diversity of genera, many of them clearly very primitive relative to *Smithistruma*, and others occupying intermediate or higher phyletic positions (Fig. 5). The Dacetini therefore provide excellent opportunities for the study of the phylogeny of predatory behavior.

During the past ten years the present authors have been conducting such a study intermittently while engaged in laboratory and field work in the United States and in both the Old and New World tropics. The following paper constitutes a preliminary summing up of the results of this effort. In it we have tried to sketch some of the evolutionary trends thus far noted and to show how much of major dacetine evolution can be interpreted as the outcome of a primary adaptive shift toward cryptic foraging that characterizes upper phyletic lines of this tribe. Of equal importance, we have attempted to indicate the large gaps remaining in our knowledge of this interesting group of insects. The possibilities for future research seem to be great, both for the evolutionist and for the physiologist interested in the analysis of stereotyped behavior.

In the descriptive parts to follow, it has been necessary to use several technical words ordinarily found only in rather specialized entomological and taxonomic literature. For the convenience of the general reader, some of these terms are briefly explained below.

Alitrunk. The central portion of the body of the ant (and other Hymenoptera), consisting of the true thorax and the first true abdominal segment, which is fused with it.

Epigaeic. Foraging in the open, whether on the ground or arboreally; contrasted with *hypogaeic*.

Foveate. Referring to integumental sculpture consisting of foveae, relatively large circular depressions with well defined margins, often bearing a hair on a central tubercle.

Funiculus. The series of segments of the antenna beyond the elongate first segment, or *scape*.

Gaster. The last major portion of the body; in dacetines the gaster follows the postpetiole and is composed of the fourth and succeeding true abdominal segments.

Hypogaeic. Foraging in hidden places, either within or beneath covering objects such as leaf litter, moss, or rotting wood (*cryptobiotic*), or deeper within the soil itself (*subterranean*).

Morphocline. A stepwise series of changing manifestations of a given character as followed through a group of related species, usually interpreted as the result of evolutionary succession.

Petiole. The first segment or node in the ant's "waist"; the second true abdominal segment.

Postpetiole. The second segment of the ant's

FIG. 1. *Daceton armigerum* (WORKER)

The large primitive dacetine is holding a small acridioid grasshopper it has just caught in its mandibles. About 10 × natural size, this remarkable photograph was taken from life near Pucallpa, Peru, by Dr. E. S. Ross. It constitutes the second known prey record for *Daceton*.

"waist" in groups, such as the Dacetini, possessing a two-jointed waist, the third true abdominal segment.

Punctuation. Referring to integumental sculpture consisting of punctures or small pits.

Scape. The elongated first (basal) segment of the antenna in ants and some other insects.

ECOLOGICAL SYNOPSES OF THE DACETINE GENERA

In the following section are listed all of the known subtribes and genera of the Dacetini, with very brief general statements concerning our present knowledge of their distribution and natural history. Most of these groups have been treated in more detail in the taxonomic and ecological papers cited at the end of the individual synopses. The number of species known in each genus is given in parenthesis *(n)* after the generic name.

Subtribe Dacetiti

Daceton (1). Neotropical. Tropical rain forest. Workers polymorphic, long-mandibulate. Nests in hollow tree trunks. Foraging epigaeic-arboreal. Food: tabanid fly (Brown, 1954a), small acridid grasshopper nymph (see Fig. 1); workers attend coccids on cacao (Bodkin in Crawley, 1916).

Acanthognathus (3). Neotropical. Tropical rain forest. Workers monomorphic, long-mandibulate. Nests in rotting logs. Foraging behavior unknown (Mann, 1922; M. R. Smith, 1944); Fig. 3.

Subtribe Orectognathiti

Orectognathus (13, including 2 undescribed). Australian-Melanesian. Warm-temperate and tropical forests. Workers primitively monomorphic, in one species secondarily polymorphic; long-mandibulate. Nests in soil and rotting wood. Foraging epigaeic, probably mostly subarboreal and nocturnal. Food: the single species studied (*O. clarki* Brown) accepted entomobryomorph and symphypleonan collembolans (Brown, 1953a, 1953b, 1958a); Fig. 4.

Arnoldidris (5). Papuan. Tropical rain forest. Workers monomorphic, long-mandibulate. Nests in soil. Foraging diurnal, chiefly subarboreal. Food: unknown. (Brown, 1958a); Fig. 2.

Subtribe Epopostrumiti

Epopostruma (6–8). Australian. Warm-temperate forest. Workers monomorphic, long-mandibulate. Nests in soil. Foraging epigaeic, terrestrial and subarboreal. Food: entomobryomorph and symphypleonan collembolans and sugary substances. (Brown, 1954a); Fig. 6.

Hexadaceton (1). Australian. Arid scrub. Workers monomorphic (?), long-mandibulate. Nesting and foraging habits unknown (Brown, 1948, 1954a); Fig. 9.

Mesostruma (2). Australian. Arid scrub to tropical forest. Workers feebly polymorphic, with mandibles of intermediate length. Nesting and foraging habits unknown (Brown, 1952b); Fig. 7.

Colobostruma (including *Alistruma* and *Clarkistruma*) (13, including several undescribed). Australian-Papuan. Arid heath to tropical rain forest. Workers monomorphic, short-mandibulate. Nests in soil and rotting wood, one species (*C. alinodis* Forel) nests with species of *Rhytidoponera*. Foraging behavior diverse; some species are hypogaeic, others epigaeic and subarboreal; some of the latter are nocturnal. Food: in two cryptobiotic species studied, entomobryomorph collembolans. (Brown, 1954a); Figs. 8, 10, 11.

Microdaceton (2–4). Ethiopian. Workers monomorphic, long-mandibulate. Primarily forest-dwelling. Nesting and foraging behavior unknown.

Subtribe Strumigeniti

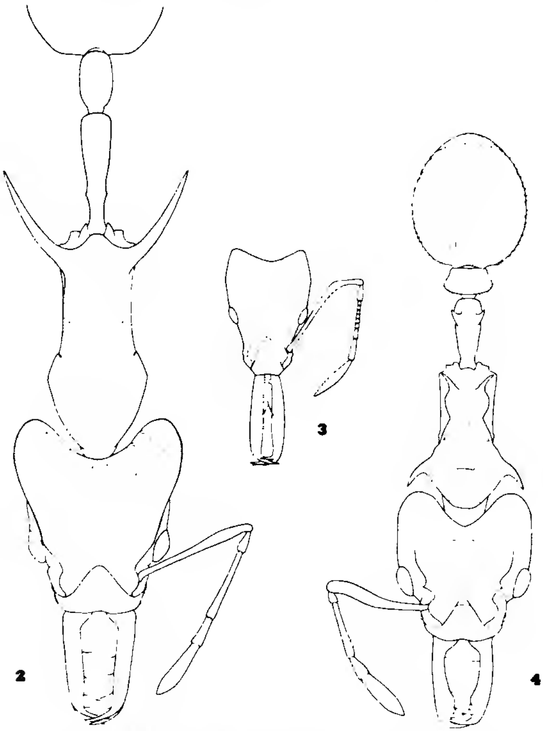
Strumigenys (including *Labidogenys* and *Pyramica*) (ca. 150). Widespread in tropics and warm temperate areas. Primarily forest-dwelling; some species occur in grassland and arid scrub. Workers monomorphic, in one species secondarily polymorphic, long-mandibulate. Nests mostly in soil and rotting wood; a few species live in arboreal plant cavities in tropical rain forest. Foraging hypogaeic to epigaeic-arboreal. Food: most species are collembolan feeders; a few are polyphagous predators (see below) or occasionally feed on sugary substances; one species (*S. xenos* Brown) is a workerless parasite. (Weber, 1939, 1952; Wilson, 1950, 1954; Brown, 1954a, 1954b, 1955); Figs. 12, 13, 17–21, 25, 26, 30, 31.

Quadristruma (artificial genus containing two species derived independently from *Strumigenys*, to be revised shortly). Workers monomorphic, short-mandibulate. One species, *Q. emmae* (Emery), is a pantropical tramp, nesting in rotting wood, coconut husks, soil, etc. Foraging behavior unknown (Brown, 1949, 1954b).

Neostruma (6). Neotropical, mainly forest floor-dwelling. Workers monomorphic, very small, mandibles varying from short-intermediate to long. Nests in rotting wood in soil cover, including small chips. Foraging (*N. mustelina*) mostly cryptic, sluggish, with "ambush" tactics frequent; utilizes "strike-hold-sting" technique of prey capture. Food, so far as known, is entomobryoid Collembola. (Brown, 1948, a revision of this genus by Brown is being readied for press.) Figs. 14–16, 32.

Smithistruma (60±). Widespread in tropics and warm temperate areas throughout world except for Australia, New Zealand, and Chile. Mostly forest-dwelling. Workers monomorphic, short-mandibulate. Nests in soil and rotting wood; a few species live in arboreal plant cavities in tropical rain forest. Foraging mostly hypogaeic, with a few species presumably epigaeic-arboreal. Food: species range from strict collembolan feeders to polyphagous arthropod predators. (Wesson, 1936; Wesson and Wesson, 1939; Brown, 1953a; Wilson, 1954); Fig. 23.

Glamyromyrmex, *Codiomyrmex*, *Codioxenus*, *Weberistruma*, *Borgmeierita*, *Pentastruma*, *Gymnomyrmex*, *Tingimyrmex*, *Miccostruma*. This is



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FIGS. 2–4. SOME PRIMITIVE DACETINE GENERA

Dorsal views, one antenna omitted in each figure. Fig. 2. *Arnoldidris szentivanyi*, worker, legs and posterior part of gaster omitted. Fig. 3. *Acanthognathus ocellatus*, head of worker. Note basal teeth of mandibles, in this genus used to carry the larvae, and the folded trigger hairs, here situated on the mandibles so as to erect and point forward when the mandibles are opened. Fig. 4. *Orectognathus phyllobates*, worker, legs omitted.

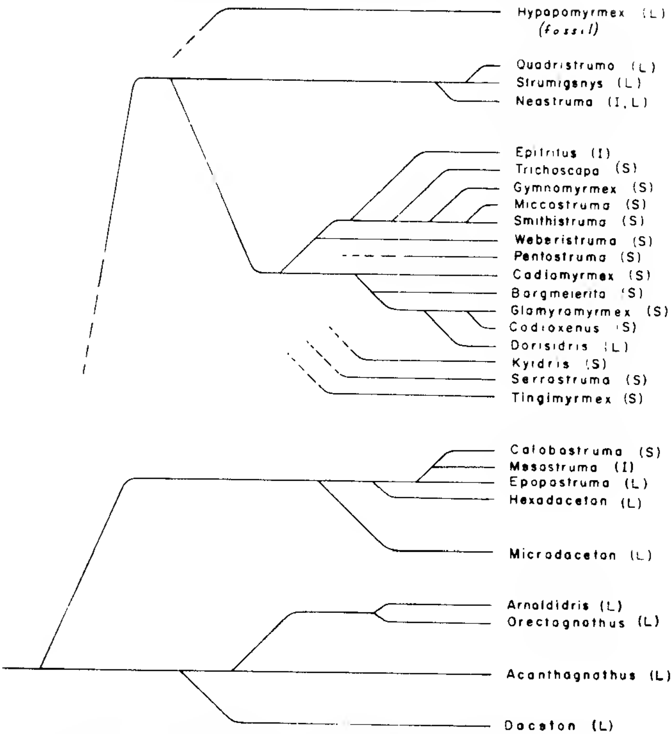


FIG. 5. PRESUMED PHYLOGENY OF THE KNOWN GENERA OF LIVING AND FOSSIL DACETINI
Letters in parentheses refer to kind of mandibles: L, long; I, intermediate; S, short

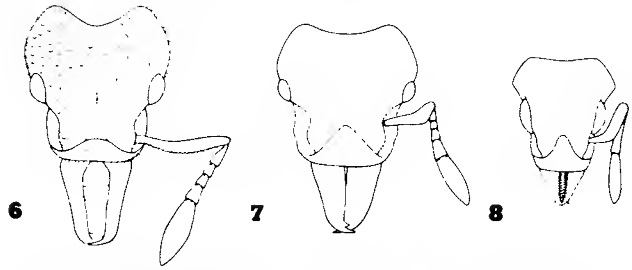
a group of genera related to *Smithistruma* and containing in the aggregate approximately twenty small, short-mandibulate, mostly tropical species. The natural history of these genera is very poorly known. (Brown, 1948, 1950, 1953a; Borgmeier, 1954); Fig. 22.

Dorisidris (1). (A long-mandibulate form derived from the short-mandibulate *Glamyromyrmex*). Cuban. Tropical deciduous forest. Workers monomorphic, long-mandibulate. Nests in soil or soil cover. Foraging behavior unknown. (Brown, 1950)

Trichoscapa (1). Widely spread by commerce through warmer parts of world, probably originating in Africa. Workers monomorphic, short-mandibulate. Highly adaptable, often living in cultured areas. Nests in soil, rotting wood, etc., often in relatively dry situations. Foraging hypogaeic. Food: polyphagous arthropod predator. (Brown, 1948, 1949; Wilson, 1954).

Serrastruma (4–6). Ethiopian-Malagasian. Highly adaptable, occurring from savanna to tropical rain forest. Workers monomorphic, short-mandibulate. Nests in soil and rotting wood. Foraging behavior unknown. (Brown, 1952a; Weber, 1952).

Epitritus (2). Mediterranean area and Japan. Workers monomorphic; mandibles intermediate in length, this condition apparently derived secondarily in evolution from short-mandibulate type. Natural history poorly known. (Brown, 1949, 1958b). Fig. 24.



FIGS. 6–8. EVOLUTION OF HEAD AND MANDIBLES IN THE SUBTRIBE EPOPOSTRUMITI

Heads of workers, dorsal view, right antenna omitted in each figure, sculpture and pilosity omitted in Figs. 7 and 8. Fig. 6. *Epopostruma* sp. Fig. 7. *Mesostruma turneri* (syntype); in this genus, mandibles basically of the *Epopostruma* type are shortened, broadened, and filled in by translucent lamella, through which the basic core shape is still visible. Fig. 8. *Colobostruma cerornata*, worker, the new inner mandibular margin has now developed serial dentition (compare with evolution of short mandibles in *Neostruma*, Figs. 13–15 and 30–33). Note the "countercurrent" development of huge eyes in this nocturnal, foliage-foraging species.

Kyidris (3). New Guinea and Formosa to Japan. Tropical rain forest and warm temperate forest. Nests in rotting wood. Workers monomorphic, short-mandibulate. The two New Guinea species are permanent parasites of *Strumigenys loriae* Emery. Workers show degenerate behavior: they do not participate in nest-building but do help their hosts with brood care and in foraging; in the latter task they are notably inefficient in comparison with the host workers. On the other hand, the parasite workers attend coccids within the nest, a function the host workers are not known to perform (Wilson and Brown, 1956).

EVOLUTIONARY TRENDS: BEHAVIORAL CHARACTERS IN THE COADAPTIVE SYSTEM

Since their origin, which presumably occurred sometime in the early Tertiary, the dacetine ants as a whole have shown an evolutionary tendency to shift from above-ground, subarboreal foraging to cryptic, chiefly terrestrial foraging. Such a trend is not unusual in the ants. It is also well marked, for instance, in the primitive tribes Ponerini and Ectatommini. Some previous authors (e.g., Haskins, 1939) have offered the interesting theory that this trend in the Ponerini has resulted indirectly from competition with more recently ascendant, dominant epigaeic groups in the Dolichoderinae and Formicinae. A similar explanation can be entertained with respect to the history of the Dacetini as against other myrmicines and the formicines, but the theme we wish to develop here is that this major adaptive shift, whatever its ultimate causation, has had a profound and pervasive influence on the course of evolution in the tribe. A number of major morphological and ethological characters have been greatly modified, apparently at least in part as a result of the change in foraging behavior. Together these form a relatively closely knit coadaptive complex of evolving characters. The specific ethological characters involved are the following:

1. *Change in hunting behavior.* The relatively primitive long-mandibulate forms rely greatly on the violent, trap-like action (Figs. 17–21) of their mandibles to secure prey, while their "approach period" toward prey is relatively short, and their use of the follow-through stinging thrust is not invariable. The short-mandibulate forms, on the other hand, have less shocking-power in their mandibles and rely more on stealth in approaching prey, in tenacity of grip following the mandibular strike, and in immediate, consistent, and efficient use of the sting. The essential features of this evolutionary change can be illustrated in the contrast between the behavior of *Strumigenys louisianae* Roger, a relatively primitive, long-mandibulate strumigenite and that of the phylogenetically more advanced, short-mandibulate *Trichoscapa membranifera* (Emery), as described by Wilson (1954):

> The *Strumigenys* are bolder and more direct in their manner of stalking prey. . . . This trait is perhaps a result of their more efficient mandibles,

which are extremely long and supplied with prominent apical teeth. They can be opened to almost 180° and operate very much as miniature animal spring traps. [Note: Recently we have discovered that the mandibles are locked into open position when special teeth at their bases catch on the lateral labral lobes; see Figs. 17–21.] When approaching a collembolan, the worker *Strumigenys* moves slowly and cautiously, spreading its mandibles to the maximum angles and exposing two long hairs which arise from the paired labral lobes. These hairs extend far forward of the ant's

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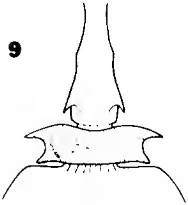

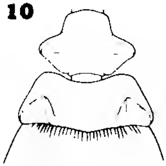

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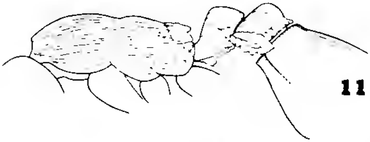

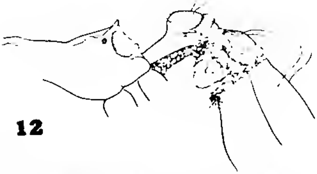

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FIGS. 9–12. INDEPENDENT EVOLUTION OF SPONGIFORM APPENDAGES IN THE TWO SUBTRIBES EPOPOSTRUMITI AND STRUMIGENITI

Fig. 9. *Hexadaceton frosti*, holotype worker, dorsal view of petiole, postpetiole and gaster. Fig. 10. *Colobostruma australis*, worker, same. Note the partial transformation of the postpetiolar teeth into submembranous alae; the smaller alae on the petiole have evidently arisen de novo, and the dorsal teeth of *Hexadaceton* have been lost. Fig. 11. *Colobostruma cerornata*, worker, side view of mid-section of body, showing the extreme development of spongiform appendages reached in the epopostrumite line. Fig. 12. *Strumigenys 'acacoca*, worker, side view of mid section of body, showing well-developed spongiform appendages of a type frequent in the strumigenite line. Evolutionary steps leading to the strumigenite appendages are unknown, but the steps represented by the epopostrumite species of Figs. 9–11 suggest one way they may have developed in the strumigenite line as well.

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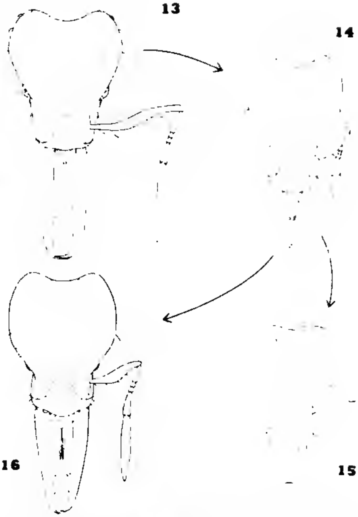


FIGS. 13–16. EVOLUTION OF THE HEAD, MANDIBLES AND ACCESSORY STRUCTURES IN THE GENUS *Neostruma*

Fig. 13. *Strumigenys jamaicensis*, worker, a member of the *S. gundlachi* group, ancestral to *Neostruma*. Fig. 14. *N. zeteki*, worker. Fig. 15. *N. metopia*, female, funicular segments of antenna omitted. Fig. 16. *N. myllorhapha*, worker. Right antenna omitted from each drawing. The paired labral lobes (between the bases of the mandibles) are short in *Strumigenys*, and the trigger hairs, which act as range-finders to set off the spring-snap action of the mandibles, are long. With the shortening of the mandibles in *Neostruma*, the labral lobes have extended and the trigger hairs have been reduced (Figs. 14, 15), presumably in order better to withstand damage from the violent struggling of the collembolan prey. In *N. myllorhapha* (Fig. 16), the mandibles are secondarily elongate, with the labral lobes further elongated to make up for the shortness of the trigger hairs. Note the correlated changes in length of the apical segments of the antennae in Figs. 13, 14 and 16.

head and apparently serve as tactile range finders for the mandibles. When they first touch the prey, its body is well within reach of the apical teeth. A sudden and convulsive snap of the mandibles literally impales it on the teeth, and drops of hemolymph often well out of the punctures. If the collembolan is small or average in size, the ant lifts it into the air [and then may sting it]. All but the largest Collembola are quickly immobilized by this action, and struggling is feeble and short lived.

As soon as the [*Trichoscapa membranifera*] worker becomes aware of the presence of a collembolan,

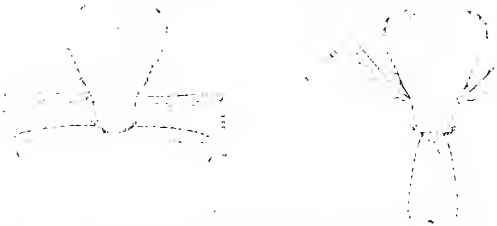


FIG. 17. *Strumigenys ludia* WORKER
Dorsal view of head, showing the mandibles in the open (left) and closed (right) positions

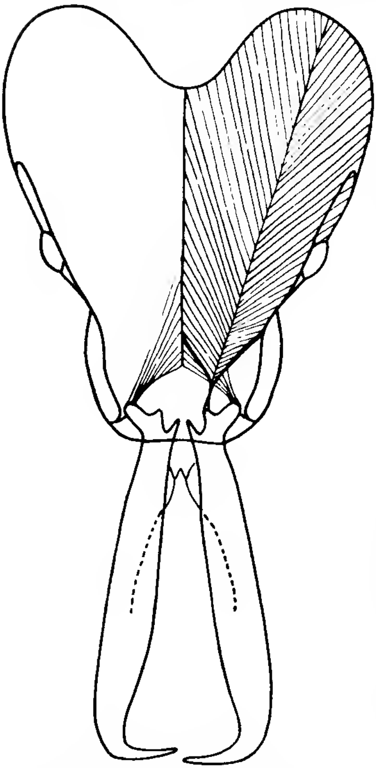
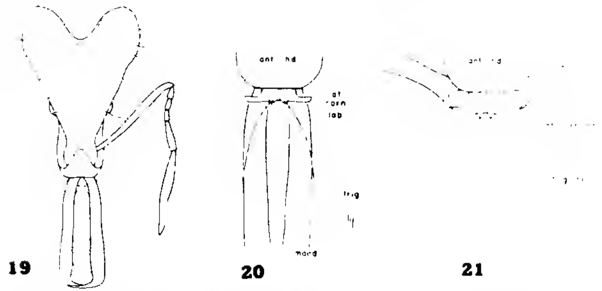


FIG. 18. *Strumigenys ludia* WORKER
Diagrammatic dorsal transparent view of head to show the approximate relationships of the mandibles to the muscles moving them. The large dorsal muscle is the left retractor; this has been removed on the right side to show the much smaller abductor muscle originating on the ventral midline of the head.

it "freezes" in a lowered, crouching position and holds this stance briefly. If the collembolan is to its back or side, the worker now turns very slowly to face it. Once it is aligned with the collembolan, it begins a forward movement so extraordinarily slow that it can be detected only by persistent and careful observation. Several minutes may pass before the ant finally maneuvers over less than a millimeter's distance to come into a striking position, and it may remain in this position for as much as a minute or more. . . . Unlike the *Strumigenys*, the *Trichoscapa* open their mandibles only to about a 60° angle. Tactile labial hairs are present and eventually come to touch the prey. The mandibular strike is as sudden as that of the *Strumigenys*, but since it is usually directed at an appendage, it does not have the same stunning effect on the collembolan. These insects often struggle vigorously to escape, but the ants are very tenacious and retain a fast grip until they are able to sting their prey into immobility.

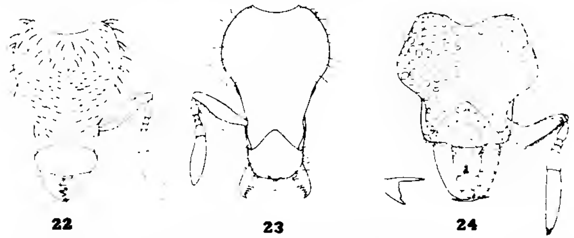
In summary, *Strumigenys louisianae* relies on a comparatively swift approach to its prey followed by a fixed-action pattern that can be characterized as *strike-lift-sting*, with the last element occasionally being omitted if the prey is small, while *Trichoscapa membranifera* employs a more cautious approach followed by *strike-hold-sting*, with the last element inevitable. It should be noted further that in *Trichoscapa* the stinging thrust follows the mandibular strike much more quickly and is apparently generally more effective than in *Strumigenys*. Both patterns, however, are individually effective in collembolan predation. The *Strumigenys* pattern is apparently typical for long-mandibulate dacetines generally, while that of *Trichoscapa* is typical for the short-mandibulate groups. The *Trichoscapa* pattern, requiring less space for the operation of the mandibles, is generally associated in the Dacetini with cryptic foraging.

Those dacetines that feed mainly on Collembola all show a relatively slow-motion,



FIGS. 19–21. THE TRAP-JAW APPARATUS OF A WORKER OF *Strumigenys louisianae*

Fig. 19. Dorsal view of head, right antenna omitted. The lateral cornuae of the labrum extend slightly beyond the lateral borders of the closed mandibles near their bases. Fig. 20. Ventral view of anterior part of head (ant. hd.) showing basal halves of closed mandibles (mand.), lateral cornuae of dropped labrum (lat. corn. lab.), and trigger hairs (trig. h.). Fig. 21. Same, open position of mandibles. When the trigger hairs are stimulated, the labrum drops down and allows the tension of the retractor muscles to pull the mandibles shut with a snap.



FIGS. 22–24. REPRESENTATIVE HEADS OF SPECIES IN THE SHORT-MANDIBULATE STOCK OF SUBTRIBE STRUMIGENITI

Workers, dorsal views of head and mandibles. One antenna omitted in each figure. Fig. 22. *Codiomyrmex semicomptus*. Fig. 23. *Smithistruma weberi*, pilosity omitted, except for fringing hairs; the mandibles are open, and the tips of labral trigger apparatus are seen projecting from beneath the clypeus. Fig. 24. *Epitritus hexamerus*, pilosity omitted from right mandible in order to show dentition. Mandibular apex in end-on view shown in inset. The mandibles and labral lobes in this genus are secondarily elongate (compare with *Neostruma mylorhapha*, Fig. 16), apparently derived from the *Smithistruma* pattern.

stealthy stalk approach to their prey, as compared to non-dacetine ants (*Hylomyrma*, *Stenamma*) that we have found to feed to some extent on Collembola also. For protection against predators, entomobryomorph springtails rely first on the fleetness of their running and their extremely sensitive and nervous escape response to movements nearby. *Hylomyrma* and *Stenamma* usually charge a springtail in a clumsy rush, with mandibles open, and this approach rarely succeeds. The collembolan simply dashes to a new position. Dacetines, on the other hand, make so stealthy an approach that the collembolans often remain undisturbed until suddenly struck by the mandibles.

Once the ant has seized the prey, the second escape mechanism of the springtail comes into play—the furcula or kick-spring organ. Used under circumstances of more violent disturbance, the furcula can project the collembolan to a considerable distance, and this movement can be made several times in rapid succession. The spring may carry the springtail away from the ant, or, if the animal is large enough, it may carry a clinging dacetine with it in its leaps and thus make the ant's return to the nest a longer and more difficult trip. It is to the ant's advantage to neutralize the action of the furcula as quickly as possible. The *Strumigenys* accomplish this by lifting their prey clear of the ground with

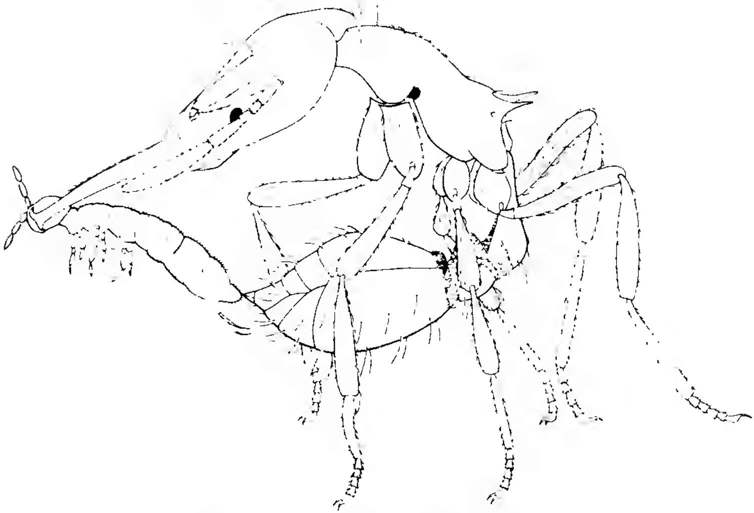


FIG. 25. A *Strumigenys ludia* WORKER STINGING A SMALL ISOTOMID COLLEMBOLAN
The ant has caught the springtail with a convulsive snap of the mandibles, and having lifted it clear of the ground, it draws its gaster under and stings its prey to render it immobile.

their long mandibles, so that the furcula cannot contact the substrate and launch the animal. If the collembolan is not killed outright by the mandibular strike, it struggles, and the ant employs the sting by reaching all the way up to the springtail with its gaster (Fig. 25). The short-mandibulate forms must depend on immobilizing their prey with a quick sting. Often the collembolan is able to make several jumps before it succumbs, but the bulldog-like tenacity of the ants usually serves to carry them along until the poison acts.

We have noted on a number of occasions in different *Strumigenys* and *Smithistruma* species that the act of stinging, once the body flexion is begun by the ants, is carried through to"completion," i.e., to extrusion of the sting at full flexion, even though the collembolan may have escaped partway through the act. This suggests the "consummatory behavior" of the ethologists (Tinbergen, 1951).

It is a curious fact that poduromorph Collembola despite their seeming helplessness and [illegible] locomotion are not taken by any Dacetini so far studied. In fact, even polyphagous dacetines will show definite avoidance of such poduromorphs as they may meet, including those upon which they have made more or less accidental mandibular strikes. Indications are that poduromorphs are protected against many predators, including dacetines, by effective repugnatorial substances.

2. *Change in amount of locomotory activity during foraging.* As a rule, the short-mandibulate, cryptobiotic dacetines hunt over more limited foraging territories and are less active during foraging.

A POSSIBLE ADDITIONAL ETHOLOGICAL TREND

On the basis of limited evidence, the primitive species *Daceton armigerum* (Roger) appears to be a general predator on medium-sized insects. Many of the higher dacetine species, however, are narrowly restricted in their predation, accepting only entomobryomorph and symphypleonan collembolans and avoiding poduromorph collembolans and other arthropods. These predators include members of *Epopostruma*, *Colobostruma*, *Strumigenys*, and *Smithistruma*. Also

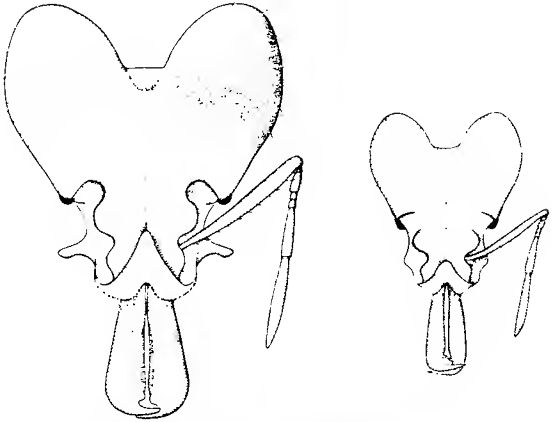


FIG. 26. *Strumigenys loriae*. SHOWING EXTREMES OF POLYMORPHISM IN THE WORKER CASTE FROM A SINGLE NEST SERIES

Note the allometric development of the mandibles and lateral genal tubercles

the relatively primitive orectognathite genus *Orectognathus* appears, on the basis of laboratory tests made on one species (*O. clarki* Brown), to be specialized to feed on collembolans. A few species of higher dacetines, e.g., *Smithistruma clypeata* (Roger), accept a small variety of soft-bodied arthropods in addition to the preferred collembolans, but can still be safely classified as oligophagous predators. The species of higher dacetines that are known to be clear-cut exceptions to the rule of oligophagy are exceptional in other ways, to the extent that they may be distinguished as members of one of the three following special classes:

(a) Possessing a polymorphic worker caste. *Strumigenys loriae* Emery, a notably polyphagous form, is the only known higher dacetine with a distinctly polymorphic worker caste (Fig. 26). (b) Widely distributed, either naturally or as tramp species carried by man. *Strumigenys louisianae* Roger ranges as a native species from the southeastern United States to temperate South America, while *S. rogeri* Emery and *Trichoscapa membranifera* Emery occur widely through the warmer parts of the world as tramp species. (c) Occurring as a member of a depauperate insular fauna. *Strumigenys nidifex* Mann, perhaps the most polyphagous of all the higher dacetines, is an exceptionally large species endemic to Fiji. A cognate species found widely from Australia to the Philippines, *S. australis* Forel, is known to be a collembolan specialist (Brown, ms.).

It would seem that the above three peculiarities are linked in some way to the condition of polyphagy. We would like to suggest, hypothetically, that polymorphism has allowed in *Strumigenys loriae* the development of a large-headed major subcaste that can capture larger arthropods; that polyphagy has allowed the wide distribution of some species by opening up to them exceptional nest sites; and finally, that *Strumigenys nidifex* has been able to expand its prey range in the absence of effective ponerine and myrmicine competitors on Fiji.

But the consideration whether these independent and secondary modifications are causally connected with polyphagy should not distract from the central question, which is whether the Dacetini were primitively polyphagous or oligophagous. Much depends on the status of *Daceton armigerum*. It can be argued that the polyphagy shown by this species, a member of one of the two most primitive living dacetine genera, is truly the primitive condition for the Dacetini, and that specialization toward collembolan predation is the derived condition. However, the opposite possibility must continue to be borne in mind. Strict collembolan feeding appears to be

characteristic of some other relatively primitive, epigaeic dacetines (*Orectognathus*, *Epopostruma*) that are widely separated phyletically. Moreover, like so many other primitive taxa, *Daceton* possesses, in addition to its truly primitive features, characters that appear to represent significant specializations away from the main line of dacetine evolution, viz., in sculpturing, worker polymorphism, cephalic articulation, and larval morphology (see Brown, 1953a; and Wheeler and Wheeler, 1954). Perhaps new light will be shed on this problem when the behavior of *Daceton* and the other living dacetite genus, *Acanthognathus*, becomes better known.

EVOLUTIONARY TRENDS: MORPHOLOGICAL CHARACTERS IN THE COADAPTIVE SYSTEM

The evolution of the Dacetini has been marked by a series of major morphological changes. Some of these are clearly coadaptive with the tendency toward cryptic foraging. Others have no known adaptive significance but are so closely associated with the major adaptive shift that they must continue to be examined in this connection.

Decrease in size. This has been a general tendency in most major groups within the tribe. As a result, the smallest dacetine workers are found in the more specialized species of the most highly evolved subtribe, the Daceti. A tendency toward small size is a general characteristic of cryptobiotic ant groups.

Shift from long to short mandibles. The primitive dacetine mandible is the long type, consisting of a linear shaft with more or less parallel margins, bearing at its apex two or three large incurved teeth. This kind of mandible is found in all four extant subtribes and is the only one in the Daceti and Orectognathiti (Figs. 1–4), in which workers and females have the primitive palpi with 5 maxillary and 3 labial segments; Daceti have 11 antennal segments, the primitive (largest) number for the tribe. In Epopostrumiti, the long mandibular type is the only one found in the otherwise generalized genera *Hexadaceton*, *Epopostruma*, and *Microdaceton*, which all have the palpi segmented 5 and 3, and the antennae 6-segmented. In the Epopostrumiti (Figs. 6–8) and Strumigeniti (Figs. 13–15, 30–33), the mandibles have evolved via different pathways to shorter types with serial dentition along their inner margins. Shortening of the mandibles in several lines in both subtribes is accompanied by reduction of antennal segmentation from 6 to 5 or 4. Presumably, the short mandibles are more advantageous in the cramped spaces hunted by the more cryptic foragers.

Reduction of palpi. This is the rule in the Strumigeniti, all of which have one short segment in each of the maxillary and labial palpi, as compared to the other subtribes, which have the segmentation 5 maxillary, 3 labial. Reduction of palpal segmentation in other ant groups is often correlated with a shift from open to cryptic foraging.

Development of antennal scrobes. The development of a longitudinal groove (scrobe) into which the antennae can be folded is well marked in some of the higher phyletic lines of the Dacetini. Scrobes are a common characteristic of other slow-moving, cryptobiotic myrmicine ants.

Reduction of the compound eyes and their ventral displacement by the antennal scrobes. These two trends are evidence of the declining role of vision in the behavior of the cryptobiotic forms.

Depigmentation. This tendency is clearly associated with cryptobiotic life in some cases, but is also occasionally associated with the secondary development of nocturnal epigaeic foraging, as in some open-country species of *Colobostruma*.

Changes in antennal form and position: reduction of segmentation, thickening of funiculus, and increasing relative prominence of terminal funicular segment. These changes, closely correlated in the higher Dacetini, are commonly seen in other cryptobiotic ants. Their adaptive significance is not well understood.

Development of bizarre pilosity. The appearance of unusual setae on the body and appendages, shaped variously to resemble threads, spoons, oars, clubs, scales, spheres, etc., is a common feature in the higher Dacetini. In earlier papers (Brown, 1950; Wilson, 1954) we have suggested that these aberrant structures might serve as tactile lures for the prey or tactile "camouflage" in cryptobiotic dacetines, but the hypothesis has not yet been adequately tested.

Modification of sculpturing. There has been a clear-cut trend in the Dacetini as a whole from coarse, foveate sculpturing to relatively fine, dense, punctate sculpturing. In a few cases (e.g. *Trnoldidris* spp., *Gymnomyrmex splendens* Borgmeier) another change has occurred: sculpturing has been lost altogether over large parts of the body. These modifications are clearly related to changes in the pilosity system of the body, which

in turn may be related to changes in the organization of mechanoreception but the matter has not been subjected to critical examination.

Development of spongiform appendages. In the Strumigeniti most of the species have developed curious symmetrical sponge-like masses on the petiole and postpetiole. Sometimes these masses are extended to the alitrunk and gaster. They are composed of integumentary outgrowths, much folded and areolated, and are sometimes associated with glandular areas. Their function is unknown. The strumigenite species that lack well-developed structures of this sort appear to have lost them secondarily. Their evolutionary origin is suggested by the morphocline produced in an independent phyletic line within the Epopostrumiti. Here are seen lateral spines transformed through a series of evolutionary steps into structures approaching in form the strumigenite spongiform appendages. (See Figs. 9–12).

Reduction of spination. This trend is shown within all phyletic lines, except the derivative Strumigeniti, the modern species of which nearly all already have the minimum fixed armament. Reduced spination is a common trait of other cryptobiotic ant groups as well as, curiously, some groups that are high arboreal and stem-dwelling (Wilson, 1959).

DIFFERENTIAL RATES IN "MAINSTREAM" AND "COUNTERCURRENT" EVOLUTION

The ethological and morphological characters described in the preceding sections show closely associated trends in their respective evolutionary histories in the principal phyletic lines of the Dacetini. Only a few examples can be cited of conspicuously differential rates in the evolution of independent characters. In the Epopostrumiti, to take a case in point, a shift from long to short mandibles is not accompanied by a significant reduction in worker eye size.

On the other hand, differential rates appear to be the rule during the short-range reversals in evolution ("countercurrent" evolution) that occur commonly in the Dacetini. Countercurrent evolution in this group has some features that deserve special attention. First, it is perhaps not too commonplace to note that the changes that occur do not represent precise reversals, in a strictly genetic sense, of the primary trends. It is noteworthy that the primary trends can be characterized generally as a movement toward specialization. The forsaking of the epigaeic foraging areas and an increased tendency toward cryptobiotic life is a derived condition for ants generally. Cryptic foraging undoubtedly opens up food and shelter niches to the higher dacetines that are but little exploited by the epigaeic forms. But it also constitutes a retreat from major niches that remain in full use (or are taken over?) by other dominant ant groups. Cryptobiotic life has been attended by some unusual evolutionary additive innovations, such as bizarre pilosity and the spongiform appendages, but in other ways it is regressive (reductive), especially where such fundamental structures as the antennae, palps, and eyes are involved. Finally, the oligophagous collembolan predation shown by many higher dacetines must be considered a specialization in the strict sense, whether it was first acquired by post-dacetite lines or by the line ancestral to all Dacetini.

Countercurrent evolution, in the cases inferred, represents for the most part a breaking-out from the narrowing adaptive zone into which higher dacetines appear to have moved. The secondary changes involved include the following: increase in size, increase in relative eye size, lengthening of the mandibles and reduction of tooth number, increase in latitude of food habits, loss of spongiform appendages, increased pigmentation (melanization) and reduction of pilosity. To cite an example, *Strumigenys nidifex*, a Fijian member of the *S. australis* group has undergone an increase in size and pigmentation and a broadening of food habits. Not all divergent trends can be considered as reversals of the primary dacetine trends. The loss of sculpturing in several groups, for instance, can be considered neither an extension of primary evolution nor a reversal of it, but rather a special trend in itself. The acquisition of worker polymorphism may fall in the same category.

Wherever countercurrent evolution has occurred, usually only a small number of characters has been involved, while others belonging to the postulated "coadaptive system" have remained relatively unchanged. For instance, in the case of *Strumigenys nidifex* just cited, size and pigmentation have been increased and food habits broadened without marked changes in other characters. The workers of certain Neotropical members of the short-mandibulate, cryptobiotic genus *Smithistruma* have taken to arboreal life in epiphyte masses, and their eyes

have been enlarged and spongiform appendages reduced; but in other characters they have remained typical for the genus. Parallel changes have occurred in some species of *Strumigenys* and *Colobostruma* (Fig. 8). A striking secondary lengthening of the mandibles and labrum has occurred in one species of *Neostruma* (Fig. 16), in *Epitritus* (Fig. 24) and in *Dorisidris nitens* (Santschi) without significant reversals in other morphological characters. In the parasitic species *Kyidris yaleogyna* Wilson and Brown, the females have lost most of their sculpturing, and the workers have undergone various degenerative changes in behavior without radical modification of most of their typical "dacetine" morphological characters.

CONVERGENCE TO THE DACETINE TYPE BY OTHER ANT GROUPS

Several other phyletic lines within the subfamily Myrmicinae show notable convergence to certain of the higher Dacetini. This resemblance is so astonishingly detailed that frequently they and their relatives have been placed by ex-

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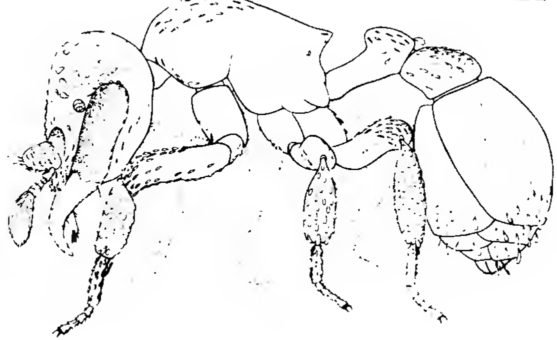

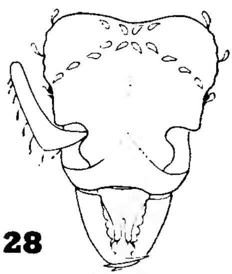

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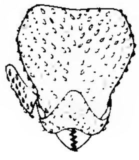

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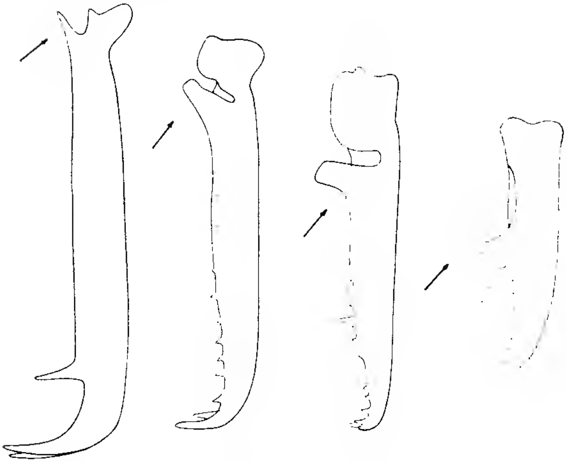
FIGS. 27–29. SOME SPECIES OF THE ANT TRIBE BASICEROTINI THAT ARE CONVERGENT TO HIGHER DACETINES

Fig. 27. *Rhopalothrix biroi*, worker, side view. A short-mandibulate form. Fig. 28. *Rhopalothrix ciliata*, worker, dorsal view of head and mandibles, antennae omitted except for right scape (compare with *Epitritus*, Fig. 24). Fig. 29. *Rhopalothrix bruchi*, same. In the Basicerotini relatively short triangular mandibles are the basic primitive type and elongate ones like those of *R. ciliata* are derived, which is the reverse of the situation in the Dacetini.



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FIGS. 30–33. PROBABLE MODE OF EVOLUTION OF THE SHORT TYPE OF MANDIBLE IN THE SUBTRIBE STRUMIGENITI

Starting with the basic *Strumigenys* type of mandible, Fig. 30, successive modifications may have led through the *S. gundlachi* group type, Fig. 31 and the *Neostruma* type, Fig. 32; to the *Smithistruma* type, Fig. 33. However, *Smithistruma* almost certainly arose from another stock of *Strumigenys*, and not via the *Neostruma* line. Note the changes in position and form of the basal tooth or lamella (arrows).

perienced systematists within the tribe Dacetini. Convergent groups include the genera *Calyptomyrmex*, *Dacetinops*, and *Rhopalothrix* (Figs. 27–29). The dacetine-like morphological characters, some or all of which are found in each of these genera, include reduction and apicalization of the antennal funiculus, reduction of palps, narrowing of the anterior portion of the head, prognathism, development of antennal scrobes, modification of sculpturing to dense punctuation, development of bizarre pilosity (especially clavate and squamate hairs), reduction of compound eyes, depigmentation, development of pedicellar spongiform appendages, and development of prominent ribbing at the base of the gaster. These characters appear to have been derived entirely independently in each group. Further, in the case of the tribe Basicerotini the known primitive members (*Basiceros*, *Aspididris*) are much less like higher dacetines than is the derivative genus *Rhopalothrix* (Brown and Kempf, 1960).

The behavior of only one of the convergent forms has been studied. Workers of the Papuasian *Rhopalothrix biroi* Emery have proven to be remarkably similar to some of the short mandibulate dacetines in their stalking behavior, and they appear to prey in large part on entomobryomorph collembolans (Wilson, 1957).

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